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REMARKABLE DEVELOPMENT OF STARFISHES ON THE NORTHWEST AMERICAN COAST; HYBRIDISM; MULTIPLICITY OF RAYS; TERATOLOGY; PROBLEMS IN EVOLUTION; GEOGRAPHICAL DISTRIBUTION

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No other part of the world, of similar extent, so far as known, has so many species of shallow water and littoral starfishes as the coasts of Alaska and British Columbia, including Puget Sound. Many of the species range from San Francisco to the Aleutian Islands, but the most favored region is from Puget Sound to southern Alaska.

The forms known to me, including those from arctic Alaska, are about eighty species, besides fifteen named varieties. No doubt special physical conditions there have favored the remarkable development of this group, as well as certain other groups, on that coast.[1]

The entire region has a very broken coast line, innumerable islands, bays, fiords and straits, giving a great extent of sheltered coast line, bathed in pure sea-water and swept by strong tidal currents, all of which are very favorable to littoral marine life, vegetable as well as animal, thus providing an abundance of food for carnivorous forms, like the starfishes, most of which feed principally on mollusks.

These favorable conditions are notably shown by the great abundance of individuals as well as species, and also by the great size that many of the species attain. At least eight of the species of Asterias and allies become there over two feet in diameter.[2]

[1] Among other groups having a similar remarkable development on that coast are the Polyplacophora (Chitons), limpets, nemerteans, tubicolous annelids (Sabellidæ), etc.

[2] Among these very large species are *Asterias columbiana* Ver., *A. Troschelii* (St.) var. *rudis* V., *A. forcipulata* Ver., *Pisaster ochraceus* (Br.),

Perhaps the relative uniformity of the temperature during the entire year is one of the most important factors in determining, or permitting, the great abundance of life on this coast, just as it is in the deep sea. Although the water is cold, it is not subject to great extremes of heat and cold, like those of the eastern coast of North America. The rapid tidal currents have a powerful effect in preventing extremes of temperature, by constantly mixing the deeper water with the shallow.

But the nature of the starfish fauna and that of other groups, like the chitons, forces us to conclude that similar favorable conditions have existed on that coast continuously for several geological periods, and that no great extermination of marine life occurred there, even during the glacial period.

A number of the genera and higher groups are peculiar to that coast; others have there a remarkable development in number and variety of species, showing that their evolution must have gone along continuously for vast periods of time. In many cases primitive and highly specialized species of a family are associated. Therefore, that coast offers unusually favorable conditions for studying the evolution of the genera and species, having there their chief development. We should naturally expect to find still surviving there, representatives of some of the comparatively early or primitive species, associated with those of more modern origin, of the same groups. Such appears to be the actual condition in many instances.

However, the complete elucidation of these questions will require a large amount of careful investigation and very extensive collections.[3]

P. giganteus (St.), *P. Lutkeni* (St.), *P. papulosus* Ver., *Pycnopodia helianthoides* St. Also *Asterias acanthostoma* sp. nov., allied to *Troschelii*, but with long proximal adambulacral spines; dorsal spines small, acute, reticulated; proximally in transverse combs; rays very long.

[3] The collections that I have personally studied are large, but not always as complete as desirable. They are from the Canada Geological Survey, the Provincial Museum of British Columbia, Washington State University, Yale University Museum, U. S. National Museum, Harriman Alaska Expedition and others.

Hybridism

One difficulty in these studies arises from the fact that certain of the species, usually very distinct, seem to hybridize in localities where their ranges overlap and the breeding seasons are coincident. Owing to the small variations in temperature the breeding season of most species is probably unusually prolonged, and this affords better opportunities for hybridization. Among such apparent hybrids, I will mention particularly those between *Asterias epichlora,* a small, usually six-rayed, diplacanthid species, and *Pisaster ochraceus* (fig. 7), a large, coarse, five-rayed, monacanthid species. The latter ranges from San Diego, Cal., to middle Alaska, and is one of the most abundant littoral species. The former ranges from Puget Sound to the Aleutian Islands. At Sitka and adjacent regions, on rocky shores, it is one of the very abundant littoral species. Although normally six-rayed, five-rayed specimens are common. It is one of those species that have the habit of carrying the eggs and young attached in clusters around the mouth.

From Sitka, Wrangel, etc., I have had a considerable number of specimens that appear to be true hybrids between these two very diverse species. They generally have the small size and form of *epichlora,* but some have the reticulated and nodular arrangement of the dorsal spines of *ochraceus.* And what is still more striking, several of them, looking like true *epichlora,* have more or less of the huge, sessile, dentate, dermal pedicellariæ (fig. 7) characteristic of *ochraceus* and the other species of Pisaster.

I have named six marked varieties of *epichlora,* which do not seem to depend on hybridization; or at least I could not satisfy myself of it. But those that I consider hybrids do not conform to any of the determinate varieties. However, it is easy to understand that if hybrids occur, as I believe they do, between *A. epichlora* and *A. hexactis,* which are much more closely allied and also occur commonly together, it would not be easy to determine the fact. The same would be true in the case of hybrids between either of the latter and *A. Troschelii,* another commonly associated species at Sitka, etc. For although the latter is a large, five-rayed species, with long rays, when young it often closely resembles some varieties of *epichlora*. Therefore it is not very unlikely that some of the so-called varieties of the latter may also be hybrids. More extensive collections with minute comparisons can alone determine such questions.

The number of species of starfishes on that coast of the family Asteriidæ (usually referred to the genus Asterias), known to me is forty, with twelve named varieties. With so many species, many of them with overlapping ranges, numerous hybrids are likely to occur. The same remarks would, most likely, apply to certain groups of mollusks, annelids, etc., in which large numbers of species occur together.

Multiplicity of Rays

So far as known to me, no other region can be compared with the northwest coast, in respect to multiplicity of rays. It is particularly noticeable in the Asteriidæ, a family that is generally five-rayed in all other parts of the world, though there are many exceptions.[4]

On the northeast coast of America there are only two exceptions: *Asterias polaris,* with six rays (Labrador and northward), and *Stephanasterias albula,* with six to nine rays, and autotomous; (from New England northward). Of the forty northwest American species of Asterias and Pisaster, twelve, or thirty per cent., have normally six rays.[5]

Besides these, the remarkable related genus, *Pycnopodia,* is peculiar to that coast. Its single species, *P. heli-*

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[4] It is also noteworthy that the genus Heliaster with several species, having from twenty-four to fifty or more rays, is peculiar to the Pacific coast of America (Lower California to Peru). The record of one species from Hawaiian waters is probably an error.

[5] Among these are *Pisaster giganteus* (St.), *A. polythela* Ver., *A. hexactis* (St.), *A. æqualis* (St.), *A. epichlora* (Br.), *A. polaris* var. *acervata* (St.), *A. macropora* Ver., *A. Katherinæ* Gray, *A. dubia* Ver. = *A. Katherinæ* Per., *non* Gray.

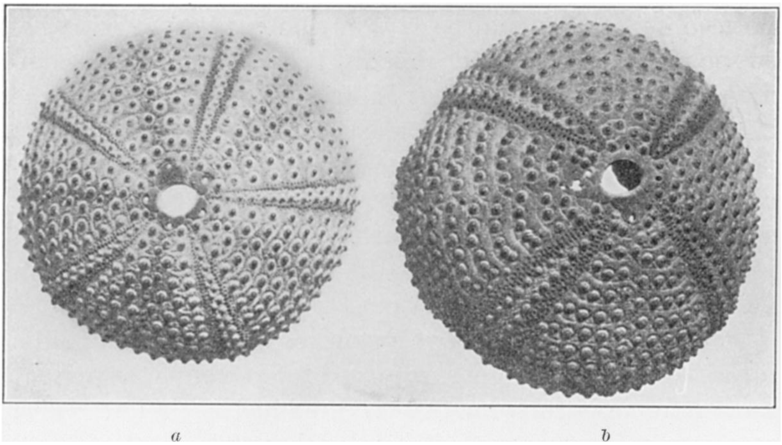

FIG. 1.—*Arbacia æquituberculata*; *a*, normal form; *b*, quadriradial specimen.

anthoides, which ranges from California to middle Alaska (Yakutat, etc.), has, when adult, twenty to twenty-four rays. It begins life as a five-rayed or six-rayed star, but acquires new rays, by budding in new rays, a pair at a time, symmetrically and side by side in succession.[6] This process is not known to occur in any other starfish, except in Labidiaster, which is an Antarctic genus of the family Brisingidæ. Several peculiar Antarctic starfishes seem to be allied to north Pacific forms.

But even those species of Asterias, etc., that are ordinarily five-rayed, occur not very rarely with six rays,[7] and the six-rayed species may occur with five rays (see note, teratology). In other families the same peculiarity is

[6] See Professor W. E. Ritter and G. R. Crocker (*Proc. Washington Acad. Sci.*, Vol. II, pp. 247–274, 1900), who give a good account of the process. I have observed many examples like theirs, but have also studied some in which there were five primary rays, and a few in which some new rays were produced, also, at irregular places, but this is unusual.

[7] I have recently collected many specimens of the very common five rayed New England species, *A. Forbesii*, near New Haven, Conn., which have four rays and six rays, and some that have seven, eight and even nine rays, by examining many thousands. About 1 in 2,000 has six rays; 1 in about 3,000 is four-rayed; 1 in about 10,000 is seven- or eight-rayed, at this time and place. Some of those with more than six rays may be due to complete repairs of injuries received in early life, with development of extra rays. (See H. I. King, "Regeneration in *Asterias vulgaris*," *Arch. Entwickel. Organ.*, IX, pp. 724–730, 1900). But this is evidently not the case with most of the four-rayed and six-rayed instances.

noticeable. Thus the peculiar genus Pteraster, which carries its young in a dorsal marsupial pouch, is found all around the world, rather sparingly, and with one exception[8] all the known species have until now, been five-rayed. The very young, taken from the pouch, agree in number of rays with the mother. On the northwest coast six shallow-water species are known, besides an additional allied genus.[9] One of these (*P. octaster* Ver.) has eight rays; another six rays.

Of Solaster, five shallow-water species are known. Of these, one (*S. constellatus* Ver.) seems to have, normally, but eight rays, an unusual number in the genus. The others have from nine to thirteen rays, the number varying in each species.

TERATOLOGY

Besides the species that normally have an increased number of rays, or vary indefinitely, there are others which have, more or less rarely, a smaller or larger number, as monstrosities. I propose to mention here a few such cases. Various other monstrous variations occur somewhat frequently, such as forked rays, supernumerary rays arising from the dorsal surface, etc. But these will mostly be discussed elsewhere.

The common large *Asterina miniata*, which ranges from south of San Francisco, Cal., to middle Alaska, becomes 175 mm. in diameter. It is normally five-rayed, but I have studied more than a dozen six-rayed specimens (fig. 2), which are regular and normal in all other respects; some are of full size; most of the large six-rayed ones were collected at Ocean Grove, Ore., by Professor W. R. Coe. In the same lot was one four-rayed specimen, 135 mm. in diameter. It is a little irregular, the greater part of one ray having been reproduced, but not to full size.

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[8] *Pteraster (Hexaster), obscurus* (Per.) = *Temnaster hexactis* Ver., has normally six rays (rarely seven). It is from Newfoundland Banks and Arctic ocean. Two other shallow water species occur on the New England coast, both five-rayed.

[9] This genus *Pterasterides* Ver. nov. is proposed for *P. aporus* Ludwig. It is peculiar in having no dorsal osculum and in having spines around the central nephridial pore that do not reach the marsupial dorsal membrane.

Dermasterias imbricata is a common five-rayed or pentagonal species, but we have one regular, six-rayed, young specimen from Sitka. The majority of our specimens have numerous large bivalve and trivalve pedicellariæ in rows, below, and smaller ones dorsally, though most writers describe it as destitute of pedicellariæ. A regular six-rayed *Henricia læviuscula* from Alaska occurred, and also a six-rayed *H. sanguinolenta* var. *pectinata* from Bering Sea.

Solaster Stimpsoni Ver. = *Crossaster vancouverensis* De Loriol, 1897. One specimen of this species from British Columbia has one of the rays forked below, near the mouth, thus producing ten regular rays as seen from above; the forking affects the ambulacral groove and jaw, the corresponding jaw being nearly abortive. The number of rays varies from nine to eleven.

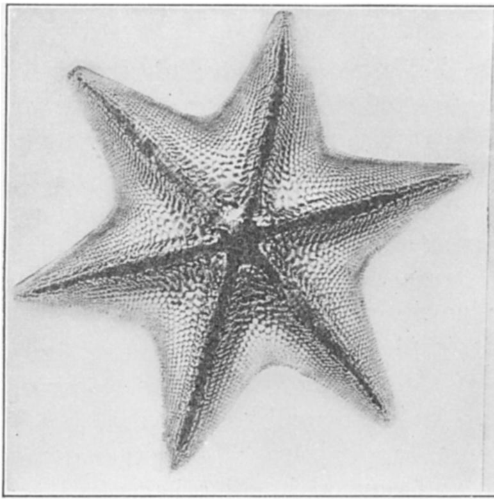

FIG. 2.

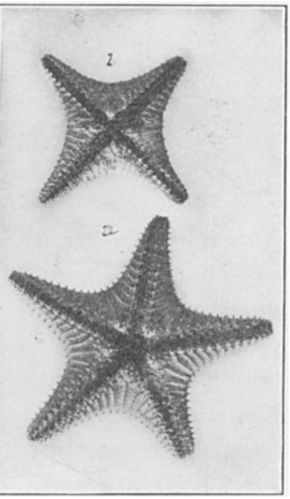

FIG. 3.

FIG. 2.—*Asterina miniata*; 6-rayed example, reduced.
FIG. 3.—*Ctenodiscus cristatus*; *a*, normal, underside; *b*, 4-rayed.

Pisaster ochraceus (Br.). One medium-sized specimen from Monterey and a large one from British Columbia have six regular rays.

Asterias (*Leptasterias*) *hexactis* (St.). Several five-rayed specimens from Sitka agree with the typical six-rayed ones in size and structural details. One from Vancouver Island has seven regular rays.

Asterias epichlora (Brandt). Although this species was originally described as five-rayed, its normal, or most common condition is six-rayed (var. *alaskensis* Ver., var. nov.), with a more or less evident median dorsal row of small capitate spines, and numerous smaller capitate spines forming a reticulated pattern over the back.[10] One specimen from Victoria has seven rays, due to the forking of one ray about at the middle; another is regularly eight-rayed. The five-rayed form is, perhaps, rather too frequent to be classified under Teratology, but in the several collections of *epichlora* examined by me, at least 90 per cent. of the specimens were six-rayed. The young, carried by six-rayed adults, were all six-rayed.

Ctenodiscus crispatus. Of this abundant species I have from New England a considerable number of regular four-rayed specimens. The few west coast specimens are five-rayed (fig. 3, *a*, *b*).

Significance of Radial Variation; a Problem in Evolution

When we consider the geological antiquity and remarkable persistence of the five-rayed condition[11] in echinoderms, generally, it seems remarkable that so many genera and species of existing starfishes should have acquired the peculiarity of having higher numbers.

All the classes of echinoderms, except perhaps holothurians, had attained highly organized and specialized conditions even in the Ordivician period. With the exception of certain cystidians and a few true crinoids, the numerous known Silurian species of crinoids, starfishes, ophiurans and echinoids were regularly five-rayed. From the Devonian, several genera of starfishes with multiple rays are known. They have the aspect of Crossaster, Labidiaster and Cronaster. But their real affinities are doubtful. Those found in the Mesozoic and Tertiary times, with rare exceptions, are five-rayed.

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[10] Whiteaves, De Loriol (1897) and others have incorrectly identified *A. Troschelii* as this species. The five-rayed form is apparently the same as *A. saänichensis* De Loriol, described and figured in 1897, *Mem. Soc. Phys. Geneva,* Vol. XXXII, No. IX, p. 23, pl. ii (xvii), figs. 3–5.

[11] The case is analogous to that of gastropods, which in primordial times acquired the habit of forming right-handed spiral shells, which has prevailed through all the geological ages, though there are some modern families and genera that are normally left-handed, and some species that are as often left-handed as right-handed (Achatinella sp.). No good reason is known why the left-handed condition is not as good as the other.

At the present time all echinoids and holothurians are normally five-rayed. Instances of monstrous specimens with four rays or six rays are very rare in these large and universally distributed groups.[12]

The modern crinoids only rarely depart from the five-rayed condition, even as monstrosities. The ophiurans show more variation in this respect. The common genus Ophiactis, varies, when young, from six-rayed to eight-rayed in nearly all of its species. But such species are usually autotomous, and when adult become regularly either five-rayed or six-rayed.

Ophiocoma pumila, at Bermuda, is about as often regularly six-rayed as five-rayed. *Ophioglypha hexactis* of Kerguelen Island is regularly six-rayed.

I have observed a large, regular, four-rayed example of *Ophiomusium Lymani* from deep water off the New England coast, but it was selected from thousands of five-rayed ones. Other radial variations in ophiurans are known to me, but they are not common, although the species are very numerous and many are often taken in vast numbers.

Among living starfishes radial variations are far more common than in either of the other classes, as already indicated. But why this is so is a perplexing problem in evolution.

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[12] In the Museum of Yale University there is a full grown, regularly four-rayed example of the sea-urchin, *Arbacia æquituberculata* (Fig. 1, *b*), from the Azores. So far as known to me this is the only known instance in that common species.

Bell (*Jour. Linn. Soc. London*, Vol. XV, p. 126, pl. v, 1880) described a quadriradiate specimen of a sea-urchin, *Amblypneustes formosa*, but it was not quite regularly developed.

Stewart, *op. cit.*, p. 130, described a specimen of *A. griseus* with six ambulacra, but that, also, was somewhat irregularly developed.

Philippi (*Arch. für Naturg.*, 1837, III, p. 241, pl. v) described a quadriradiate *Echinus melo*, which was also a little irregular. A few other cases are known among echinoids.

No doubt there are some advantages in the five-rayed condition, or else it would not have remained so constant through all the geologic ages. But it is equally certain that it is more advantageous for certain starfishes, in their special environments, to have six or more rays, otherwise they would not have retained this condition. We must conclude that all these variations originated, at first, as "sports," which have persisted by heredity and natural selection, because they were advantageous. It is easy to conjecture that, in the case of two starfishes, similar in size and structure, living together on a rocky shore and exposed to violent surf, the one with six rays would be able to cling more securely to the rocks than the one with five rays. Therefore, because of the increased number of ambulacral sucker-feet it might well be the form preserved by natural selection, unless for some other important but unknown reason, the five-rayed condition has certain other more important advantages.

It is certainly true that most of the species with multiple rays live among rocks in situations exposed to the surf.[13] This is true of the various shallow water and littoral species of Solaster and Crossaster, which usually have nine to thirteen rays (rarely eight or less). It is also true of the several species of Heliaster with very numerous rays, and many other such species, as well as the numerous five-rayed and six-rayed species of Asterias and Pisaster.

But the power of effectually clinging to rocks may be perfected in other ways, involving an increased number of sucker-feet. This is often attained by lengthening the rays, as in many species of Asterias; by crowding the suckers into more than four rows, as in Pycnopodia and some large species of Pisaster; and by increasing the size and strength of the suckers.

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[13] The family Brisingidæ, however, is confined to deep water. All the species are multirayed, with long rays.

These same adaptations would also be useful in enabling the creatures to securely hold their prey, especially while, at the same time, holding fast to the rocks.

I am inclined to believe that the increase of rays has been due more to the advantages gained in holding the food securely than for holding to the rocks, though both go together. The starfishes are the most predacious of the echinoderms. Although they feed largely on gastropods and bivalve mollusks, they also feed on each other, and on large holothurians, echini, and other relatively large creatures.

However, we must admit that, so far as now known, the five-rayed and six-rayed individuals of a species appear to be equally well nourished and grow to equal size. Also that the normally six-rayed species of Asterias are no larger, nor more robust, than the allied five-rayed species, in the same environment. Even the four-rayed individuals, including the four-rayed sea-urchin (Arbacia), mentioned above, appear to be well fed and of average size.

Some, at least, of the many-rayed Brisingidæ use their slender rays for clinging to the deep-sea Gorgonians. I have observed that the *Odinia americana* Ver. thus clings to the branches of *Paragorgia arborea* with its twenty long rays. In such cases numerous rays would be advantageous.

It must be borne in mind that the variation in the number of rays is necessarily attended by extensive changes in the number, size and form of all the skeletal plates; also in the number of ambulacral feet and water tubes, nerve ganglions, nerve cords, stomach lobes, hepatic glands and all other internal organs. A six-rayed specimen has twelve reproductive glands, instead of the ten in its five-rayed competitor. If the number of ovules be proportionately large, it would produce twenty per cent. more young. So, likewise, it would have an additional stomach-lobe and two more hepatic glands. This would, perhaps, be of considerable advantage in the digestion of food and cause more rapid growth. We know that there is great variation in the size of different individuals of young starfishes of equal age, of the same species, dependent on temperature and relative abundance of food. But I know of no experiments or observations to connect this with the number of congenital rays.

DISTRIBUTION

A number of Arctic species occur in Bering Sea and as far south as the Aleutian Islands, or somewhat farther. Most of these are circumpolar, as *Crossaster papposus, Solaster endeca, Henricia sanguinolenta, Ctenodiscus crispatus, Asterias polaris, Asterias hyperborea* (=*A. arctica Murd.*), *A. grœnlandica*=*A. cribraria* St. and others.

Some Arctic species are peculiar to the north Pacific side, so far as known, as *Pterasterides aporus* (Ludwig), *Tosia arctica* Ver., *Asterias polythela* Ver., *Allasterias rathbuni* Verrill, *Pteraster octaster* Ver.[14] and others.

But exclusive of the Arctic forms, the entire starfish fauna of the coast, from the Aleutian Islands to San Francisco, is peculiar to that coast, so far as I can determine, and is rather sharply limited, both northward and southward by temperatures only. Some species[15] are closely related to North Atlantic ones, and evidently represent divergent groups derived from a common stock, at no very remote period. However, the cases of greatest interest are those of generic types peculiar to the fauna, some of which have no near allies elsewhere. Among such genera I may mention here a few examples: *Pyconopodia,* with no near allies; *Acantharchaster* Ver., a very isolated genus; *Dermasterias,* with a single species; *Glyphaster* Ver. (type *Leptychaster anomalus* Fisher), with

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[14] These last four species are described in the *Amer. Jour. Science,* July, 1909, with others from the same coast.

[15] Among these are *Hippasteria spinosa* Ver., closely related to *H. phrygiana; Leptychaster millespina* Ver., closely related to *L. arctica.* It differs in having smaller dorsal paxilli with fewer spinules, more transversely elongated supero-marginal plates; much finer and more numerous adambulacral spines, four or five in the furrow series. *Mediaster æqualis* St., related to *M. bairdii* V.; *Luidia foliata* Gr., allied to *L. clathrata.* Some of these were evidently derived from Arctic forms.

FIG. 7.

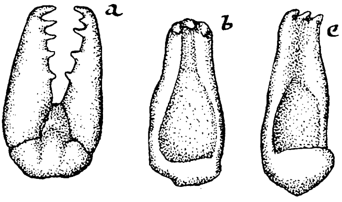
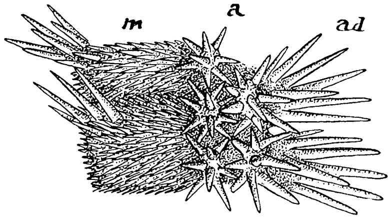


FIG. 4.



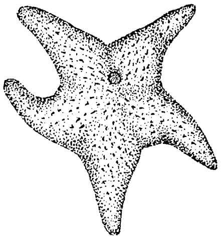


FIG. 5.

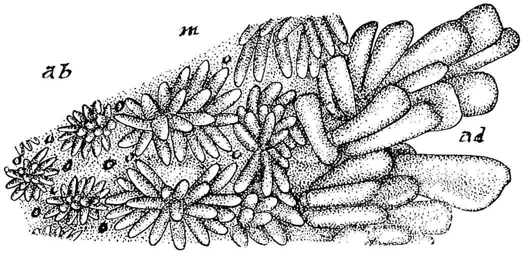


FIG. 6.

FIG. 4.—*Bunodaster Ritteri* nov.; *ad*, adambulacral spines; actinals; *m*, marginals.

FIG. 5.—*Henricia tumida* Ver. sp. nov.

FIG. 6.—*H. spatulifera* sp. nov.; *ad*, adambulacral spines; *m*, marginals; *ab*, abactinal pseudopaxillæ; much enlarged.

FIG. 7.—Large unguiculate and denticulate dorsal pedicellariæ of *Pisaster ochraceus*; *b*, *c*, separated valves.

one species (*G. anomalus*): and especially *Pisaster*, which has there eight, large, massive species (mentioned above, p. 542). I am unable to refer with certainty any of the species described as *Asterias*, from other regions, to this group, as restricted, unless it be the six-rayed species, *A. Perrieri* Smith,[16] from Kerguelen I. This agrees with it closely. It is monacanthid and has large dentate pedicellariæ.

Cosmasterias sulcifera (Per.) Sla., from southern South America, is also pretty nearly allied to Pisaster, but is diplacanthid and has few dorsal major pedicellariæ, which are not particularly large. This is the type of Cosmasterias Sla. and it seems better to keep the latter name for this and allied diplacanthid species. It is evident, however, that these Antarctic forms are the nearest relatives of Pisaster.

Bunodaster, gen. nov., resembles Astropecten, but has

[16] *Trans. Phil. Soc.*, Vol. 168, p. 273, pl. xvi, figs. 2–2*b*, 1879.

convex abactinal *pseudopaxillæ;* triangular actinal area of about three V-shaped rows of tesselated plates; curtailed inferomarginals; numerous adambulacral spines. Type *B. Ritteri,* nov. (Fig. 4), has inferomarginals with a distal group of small spines, elsewhere finely spinulose; furrow spines about five to a plate and eight to twelve on actinal side; no spines on superomarginals. California (Prof. W. G. Ritter).

The peculiar northern species, *Allasterias rathbuni,* is represented on the Asiatic coast by *A. versicolor* (Sla. sp. of Japan), which has alternately one and two ambulacral spines, and by *A. amurensis* (Lutk.), Japan to Siberia. Many of the other species of Asteriidæ are only remotely allied to those known in other faunæ. This family and the genus Asterias are world-wide in distribution, but no other region has such a variety of forms.

The family Pterasteridæ is also uncommonly well developed. Seven species have been found in shallow water, besides others in deep water. They all belong to the restricted genus Pteraster, except the remarkable form, *P. aporus* Ludwig, for which I have proposed the new genus Pterasterides (see p. 547, note). It has no dorsal osculum, and the spines around the nephridial or central pore do not reach the marsupial membrane. The Retaster, described by Clark from Puget Sound, I refer to Pteraster (*P. gracilis*). The *P. reticulatus* Ives, which ranges from Puget Sound to middle Alaska, is a very large species and is the most common one. *P. hebes* Ver. and *P. octaster* Ver. are very unlike any species from other regions.

The genus Henricia (formerly Cribrella) is also represented by numerous species and varieties. *H. tumida* Ver., from North Alaska, Cape Fox and C. Disburne, Fig. 1, is remarkable for its large swollen disk and short, stout rays. *H. spatulifera* Ver. southeast Alaska, Fig. 2, is remarkable for its broad paddle-shaped or spatuliform adambulacral spines which are much crowded proximally (see figures).